Phytologia (March 1992) 72(3):231-252.

NEW SPECIES AND TAXONOMIC EVALUATIONS OF MEXICAN CASTILLEJA (SCROPHULARIACEAE)

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ABSTRACT

Four new species of Castilleja are described from México. Castilleja jiquilpana from Michoacán is most closely related to C. scorzoneraefolia. Castilleja durangensis from Durango is most closely related to C. aspera, and C. galehintoniae from Nuevo León is most closely related to C. lanata. Castilleja dendridion from Oaxaca has much more uncertain evolutionary affinities. The identities and taxonomic status of the accepted species C. scorzoneraefolia, C. falcata, C. rigida, C. nervata, C. bella, and C. aspera, as well as taxa relegated to synonymy, are evaluated.

KEY WORDS: Castilleja, Scrophulariaceae, México

In the course of providing general identifications of recent collections of Castilleja from northern México, as well as curating LL, TEX collections of the genus, a number of taxonomic problems and undescribed taxa have come to light. A review of the genus in México and Central America (Nesom unpublished) accounts for 52 species in mainland México, an additional thirteen in Baja California (only one of these occurs on the mainland), and nine in Central America (six endemic there). Eastwood's study (1909) of Mexican and Central American Castilleia recognized 54 species, seventeen originally described by her. Brandegee (1914) described an additional species from mainland México, Standley & Stevermark (1944) one from Guatemala, Standley (1936; 1940) three species from mainland México and one (1938) from Costa Rica, the latter including three species later proposed by Pennell, Crosswhite (1970) one, Rzedowski (1975) one, Holmgren four from México (1976) and four from Costa Rica and Panamá (1978), and Moran (in Levin & Moran 1989) one from México. Breedlove & Heckard (1970) placed a new species from Sinaloa in the monotypic genus Gentrya, which has recently been positioned within

Castilleja (Chuang & Heckard 1991). Six other species have been described since 1909 from Baja California or from southern California and are known to occur in Baja California. The present study adds four new species of Castilleja from mainland México; a companion paper (Nesom 1992) adds another that is primarily centered in Texas but that also occurs in Coahuila.

Where species have been problematic in their past circumscriptions, their identity and geographical distribution are documented by specimen citations in the present study. All taxa are mapped, based primarily on specimens from GH,MO,NY, and LL,TEX.

I. The identity of Castilleja scorzoneraefolia Kunth

- Castilleja scorzoneraefolia Kunth, Nov. Gen. & Sp. 2 [folio]:267. 1818; 2
 [quarto]:331, tab. 165. 1820. TYPE: MEXICO. Michoacán: "Ario Pazcuaro" (as on the specimen), [Sep 1803], Humboldt & Bonpland s.n. (HOLOTYPE: P fiche!). The protologue: "Crescit in rupestris Novae Hispaniae prope Pazcuaro et Ario, alt 1100 hex. 4 Floret Augusto."
 - Castilleja lithospermoides Kunth, Nov. Gen. & Sp. 2 [folio]:266. 1818; 2 [quarto]:331, tab. 164. 1820. TYPE: MEXICO. Hidalgo: "Moran" (as on the specimen), [May-Jun 1803], Humboldt & Bonpland s.n. (P fiche!). The protologue: "Crescit in temperatis Novae Hispaniae prope Real del Monte et Moran, et in Regno Quitense prope Chillo, alt 1350 hex. 4 Floret Majo-Junio." The sheet of C. lithospermoides has 3 branches: the one on the left is typical C. scorzoneraefolia; the identity of the other two is more equivocal, and it is possible that they might even represent what is identified in the current study as C. nervata Eastwood. If so, however, it is not likely that they originated from central Hidalgo, which is north of the range of C. nervata (Map 1). Further, the original illustration of C. lithospermoides (tab. 164) shows a plant nearly identical to that pictured for C. scorzoneraefolia (tab. 165), the leaves with expanded and distinctly clasping bases and corollas exserted from calyces.
 - Castilleja glandulosa Greenm., Proc. Amer. Acad. Arts 41:247. 1905. TYPE: MEXICO. México: hills near Lecheria Station, 2200 m, 2 Jul 1904, C.G. Pringle 10,000 (HOLOTYPE: GH!; Isotypes: LL!, MO!).

Perennials usually from a taproot. Stems herbaceous, 10-30(-40) cm tall, erect, straight, commonly with short, eglandular, deflexed hairs, stipitate glandular hairs, and much longer, stiffly spreading, eglandular hairs; lower leaf surfaces moderately to densely hirsute with stiff, straight, eglandular hairs,



Map 1. Distribution of Castilleja nervata. C. scorzoneraefolia, C. jiquilpana, and C. dendridion. Arrows show the locations of type collections.

sometimes also with glandular hairs, the margins commonly ciliate with much longer hairs. Leaves 2-7 cm long, narrowly triangular, entire, 3 veined, the veins sometimes prominently raised, sessile, distinctly clasping. Floral bracts 24-30 mm long, oblong lanceolate to obovate, 3 veined, 5-12 mm wide, entire, the upper red tipped. Calyx red and glandular at the apex, 19-32 mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, equally divided, the primary lobes 7-12 mm long, the secondary lobes rounded and shallow, 1-3 mm long, sometimes completely absent. Corolla 21-37 mm long, the lower lip of 3(-5), thick green teeth 1-2 mm long, the galea 7-12 mm long, 30%-34% as long as the corolla, usually exserted from the calyx 3-9 mm, rarely included. Chromosome numbers, n=12 and n=24, both unpublished counts by Chuang, according to label data.

Widespread in temperate areas of southcentral to northeastern México (Map 1); (950-)1250-3590(-4100) m; Apr-Sep.

Castilleja scorzoneraefolia is one of the most common and widespread species of México. It is somewhat variable in features of vestiture, calyx morphology, and degree of corolla exsertion, but for the most part, identifications of this species are relatively consistent. Possible intermediacy between C. scorzoneraefolia and C. rigida Eastwood and C. nervata is discussed below. Numerous collections from westcentral Zacatecas and adjacent Durango appear to represent a disjunct, northwesternmost segment (Map 1) of C. scorzoneraefolia and may prove to deserve taxonomic recognition. These plants consistently produce highly glandular stems and leaves, leaves with sinuate margins, prominent axillary clusters of leaves, and calyces with red and white longitudinal stripes. Such features, however, also occur in plants scattered through the range of the species.

Eastwood (1909) distinguished *Castilleja scorzoneraefolia* from close relatives by its lower corolla lip of five teeth, three primary ones and two smaller ones in the sinuses of the others. I also have observed this feature, but it is not constant within the species. A similar lower corolla lip also occurs sporadically in plants of *C. rigida* (see below).

Plants with 3 lobed bracts and leaves, but otherwise mostly similar to C. scorzoneraefolia, occur in the high elevation regions of Veracruz (Orizaba and Perote, Map 1), where they have been named as C. falcata Eastwood. These apparently are annual or short lived perennials and are erect and single stemmed from the base. They appear to intergrade with typical C. scorzoneraefolia, but no other plants of the latter over the range of the species produce this morphology and C. falcata is tentatively maintained here as a taxon deserving recognition at least at some rank.

Castilleja falcata Eastwood, Proc. Amer. Acad. Arts 44:575. 1909. TYPE: MEXICO. Puebla: Mount Orizaba, 3660 m, 14 Aug 1901, C.G. Pringle

8560 (HOLOTYPE: GH!; Isotype: MO!).

In contrast to the somewhat ambiguous distinction of *Castilleja falcata* from *C. scorzoneraefolia*, another closely related but previously unrecognized population system appears to be clearly distinct as a species and is formally described here.

Castilleja jiquilpana Nesom, sp. nov. TYPE: MEXICO. Michoacán, 1 mi W of El Fresno, 6 mi from jct of Hwy 15 on Hwy 110, 6000 ft, 7 Jul 1966, E. Molseed 441 (HOLOTYPE: LL!; Isotypes: MO!,UC).

Castillejae scorzoneraefoliae Kunth similis sed duratione breviore, caulium vestimento sparsim piloso eglanduloso, foliorum lobis linearibus, et calycibus flavifasciatis differt.

Plants apparently annual, from a short, slender taproot. Stems 22-38 cm tall, eglandular, very sparsely pilose with vitreous, spreading hairs mostly 0.5-1.0 mm long and a sparse understory of much smaller, loose, often somewhat deflexed hairs. Leaves subclasping, lanceolate, 2-5 cm long, 2-7 mm wide (at midleaf), 3 veined with the midvein raised, at least the lower leaves with 1-3 pairs of filiform lobes from the upper half of the broad central portion of the lamina, upper leaves entire to lobed. Mature inflorescence/infructescence 8-15 mm long; floral bracts lanceolate, the lowermost sometimes lobed like the leaves, 17-25 mm long, 4-6 mm wide, the upper third red and minutely glandular. Calvx red tipped and glandular at the apex, 15-17 mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, the primary lobes 6-8 mm long, nearly equal in length, rounded at the apex with barely if at all developed secondary lobes, or shallowly notched with small but distinct secondary lobes, red on the upper fourth, green below, a yellow band ca. 1 mm wide between the red and green portions. Corolla exserted from the calvx 1-4 mm, the lower lip of 3, thick, green teeth ca. 1 mm long, the galea 6-8 mm long, 33%-45% as long as the corolla, glandular and sparsely pilose. Chromosome number, n=12 (see voucher below).

Northwest Michoacán (Map 1); wet, grassy fields and roadsides, 2050-2310 m; Jun-Aug.

Additional collections examined: MEXICO. Michoacán: Ca. 22 km W of Jiquilpán on Rta. 110, 3 Aug 1966, Cruden 1149, voucher for chromosome count of n=12, as Castilleja glandulosa [Heckard 1968] (TEX); 12-13 km W of Jiquilpán on Rta. 110, 1 Jul 1968, Cruden 1322 (NY).

Castilleja jiquilpana apparently is a narrow endemic (Map 1) in a distinctive habitat. All three collections studied were made within about 30 kilometers of each other in the area of Jiquilpán, Michoacán. The plants are similar to *C. scorzoneraefolia* particularly in their subclasping leaves and features of the calyx. The new species is morphologically distinct in its apparently annual duration (judging from the short, very slender taproot), yellow banded calyces, eglandular and sparsely pilose stems. and deeply divided leaves with linear lobes. Scattered plants of C. scorzoneraefolia throughout its range may show some of these features, but the only other plants within the C. scorzoneraefolia group with similarly divided leaves and bracts are those of C. falcata, C. moranensis Kunth, and C. bella Standley (see discussion below of the latter two).

Castilleja jiquilpana also is at least superficially similar to C. saltensis Eastwood, which is endemic to southeastern Durango. Plants of the latter, however, are shorter with floral bracts that are most often lobed (vs. entire), a more villous stem vestiture of hairs with a strong tendency to be produced in vertical lines, and calyces that lack a yellow band beneath the distal red portion.

- II. The identity of Castilleja rigida and C. nervata
 - Castilleja rigida Eastwood, Proc. Amer. Acad. Arts 44:575. 1909. TYPE: MEXICO. Chihuahua: hills near Chihuahua, 16 Apr 1885, C.G. Pringle 188 (HOLOTYPE: GH!).
 - Castilleja latebracteata Pennell, Proc. Acad. Nat. Sci. Philad. 73:533.
 1921. TYPE: UNITED STATES. Texas: Val Verde Co., High Bridge [Southern Pacific Railroad] of the Pecos, 1000 ft, 27-28 Apr 1903, Dr. H.A. Pilsbry s.n. (HOLOTYPE: PH!).

Stems woody, (15-)14-55 cm tall, commonly slightly zig-zag at the nodes. Stem and leaf surfaces softly pilose to villous with eglandular, vitreous, loosely spreading, and somewhat crinkled hairs, mixed with gland tipped hairs. Leaves obovate, sessile, not clasping, without prominently raised veins. Floral bracts entire, 3 veined, 8-16 mm wide. Calyx red tipped and glandular at the apex, 20-32(-36) mm long, from the base is somewhat constricted at ca. midlength, then broadening again toward the apex, the primary lobes lobes (5-)7-12 mm long, nearly equal in length, with rounded, barely developed secondary lobes. Corolla conspicuously exserted from the calyx, (24-)28-36(-42) mm long, the lower lip of 3(-5), thick, green teeth 0.5-1.5 mm long, the galea (8-)10-14 mm long, 33%-45% as long as the corolla. Chromosome number unknown.

Chihuahuan Desert region of Chihuahua, Durango, Zacatecas, Coahuila, and Nuevo León, México, also trans-Pecos Texas (Map 2); matorral, sometimes into mesquite or oak woods, limestone substrates. except in the igneous Santa Rosa Mountains southwest of Muzquiz; (500-)1100-2800 m; (Mar-)Apr-Oct (-Feb).



Map 2. Distribution of *Castilleja rigida*, *C. aspera*, and *C. durangensis*. Arrows show the locations of type collections.

Castilleja rigida is the earliest and correct name for the plants of trans-Pecos Texas and northern México that previously (Holmgren 1970) have been identified as *C. latebracteata* Pennell. The species is almost completely confined to the Chihuahuan Desert Region and occurs relatively abundantly in the Mexican states of Durango, Zacatecas, Chihuahua, Coahuila, and Nuevo León, as well as in southern Texas (Map 2; also see Nesom 1992). The plants are easily identified by their morphology and geographic range and I have not cited specimens.

In its calyx and corolla morphology, Castilleja rigida is similar to C. scorzoneraefolia, and the two species are almost certainly closely related. There is some indication that gene flow occurs between them where they are sympatric in Coahuila. For example, in the Sierra de la Gavia (35 mi south of Monclova), Henrickson has collected plants of C. rigida (oak woods at 4500 ft, 11777b, NY-2 sheets) with tall, slightly zig-zag stems and nonclasping leaves but atypical in their very narrow floral bracts, in close proximity to C. scorzoneraefolia (oak chaparral at 5900 ft, 11808, NY-2 sheets) with clasping leaves but tall, distinctly woody stems and wide floral bracts. Similar examples can also be found in the region of Muzquiz, Coahuila, at the northernmost extension of the range of C. scorzoneraefolia.

Castilleja rigida also has been confused with C. nervata Eastwood (in specimen annotations, by my own and those of others, the two species considered together as C. nervata). Plants of both species are strongly perennial with woody, slightly zig-zag stems and non-clasping leaves, but they are distinct from each other in both geography (Maps 1 and 2) and a number of morphological features. Both C. rigida and C. nervata are closely related to C. scorzoneraefolia. The three species are distinguished by features in the following couplet.

- Castilleja nervata Eastwood, Proc. Amer. Acad. Arts 44:574. 1909. [22 May] TYPE: MEXICO. Chihuahua: vicinity of Madera, 2250 m, May-Jun 1908, E. Palmer 274 (HOLOTYPE: GH!; Isotype: MO!).
 - Castilleja angustifolia Mart. & Gal., Bull. Acad. Roy. Sci. Brux. 12(2):29.
 1845. TYPE: not seen. Not Castilleja angustifolia G. Don, Gen. Syst. Gard. Bot. 4:616. 1838, from North America; not Castilleja angustifolia (Nutt.) A. Gray in Torrey, Bot. U.S. & Mex. Bound. Surv. 2(1):118, 1838, from North America. The identity of C. angustifolia Mart. & Gal. is accepted here fide Eastwood (1909), who noted that it is the same species as C. lithospermoides (=C. nervata in the sense of the present treatment, see comments below). The name upon which Gray's combination was based, Euchroma angustifolia Nutt., almost certainly represents some other species, perhaps C. angustifolia (Nutt.) G. Don, rather than the specimen Gray referred to, which was apparently at hand (=Castilleja integra A. Gray, a Wright collection from Texas).
 - Castilleja cryptandra Eastwood, Proc. Amer. Acad. Arts 44:578. 1909. TYPE: MEXICO. Colima: Cuchilla, NE side of Volcán Colima, 22 Jul 1905, P. Goldsmith 76 (HOLOTYPE: GH!; Isotype: MO!).
 - Castilleja cruenta Standley, Muhlenbergia 5:82. 1909 [7 July]. TYPE: UNITED STATES. Arizona: Cochise Co., Chiricahua Mountains, rocky spur N of Wilgus Ranch. rhyolite, 6000 ft, 2 Sep 1907, J.C. Blumer 2133 (HOLOTYPE: NY! ex NMC). The identity of these plants with Castilleja nervata has also been recognized by N. Holmgren, as evidenced by his 1983 annotation of the type specimen.

Stems woody, (15-)30-100 cm tall, commonly slightly zig-zag at the nodes. Stems commonly with short, eglandular, deflexed hairs, stipitate glandular hairs, and much longer, stiffly spreading, eglandular hairs; lower leaf surfaces moderately to densely hirsute with stiff, straight, eglandular hairs, sometimes also with glandular hairs, the margins commonly ciliate with much longer hairs. Leaves obovate to linear lanceolate, sessile, not clasping, the 3 major veins prominently raised on the lower surface. Floral bracts entire, 3 veined, 6-15 mm wide. Calyx green, 15-24 mm long, tubular, the primary lobes 8-14 mm long, nearly equal in length, with rounded, barely developed secondary lobes. Corolla completely included within the calyx, 15-24 mm long, the lower lip of 3, green, thickened, linear-attenuate teeth 2.0-2.5 mm long, the galea 5-8 mm long, ca. 33% as long as the corolla. Chromosome numbers, n=12, n=24 (see vouchers below).

Southern Arizona in the United States, and in the following Mexican states: Sonora, Chihuahua, Distrito Federal, Sinaloa, Durango, Nayarit, Jalisco, Colima, México, Michoacán, Guerrero, Morelos, Puebla, Veracruz, and Oaxaca (Map 1); rocky slopes or openings, oak to pine-oak or pine woods, rarely in pine-fir; 750-2300(-2600) m; (Apr-)Jul-Oct(-Nov). Eastwood (1909) noted that this species (as *Castilleja lithospermoides*, see comments below) occurs in South America, but I have confirmed its presence only in México.

Representative collections examined: MEXICO. Chihuahua: Mpio. Batopilas, N of Quirare on La Bufa-Creel road, 31 Jul 1977, Bye 7782 (GH); Mesa de Arroyo Seco, 25-30 km SW of Minaca, 16-17 Sep 1934, Pennell 18846 (GH,NY). Distrito Federal: Lomas, Sep 1930, Lyonnet 743 (MO). Durango: Along trail from Pueblo Nuevo to Cueva, 30-31 Aug 1934, Pennell 18487 (GH). Guerrero: SW of Xochipala, ca. 40.5 km SW of K236 on Rta. 95, 20 Jul 1969, Cruden 1628 (NY). Jalisco: Ca. 17.5 km S of Autlán on Route 80, 2 Aug 1969, Cruden 1672 (NY); hills near Guadalajara, 13 May 1901, Pringle 9461 (GH,NY). México: 10 mi N of México City near Atzcapotzolco, 1-15 Jul 1937, Happ 109 (MO). Michoacán: Cerro Tancitaro, 19 Aug 1940, Leavenworth 664 (NY, with Castilleja scorzoneraefolia); hills near Patzcuaro, 30 Jul 1892, Pringle 4168 (GH,MO,NY). Morelos: Cuautla, Jul 1930, Lyonnet 743 (NY); La Herradura near Cuernavaca, 14 May 1938, Williams 3048 (MO). Navarit: Cerro de San Juan, SW of Tepic, 18 Aug 1935, Pennell 19754 (GH,NY); ca. 19 km S of Tepic, 27 Jun 1968, Cruden 1313 (NY). Oaxaca: Dpt. Mixe, between San Isabel and San Juan Mazatlán, [no date], Lipp 37 (NY); Dept. Etla, 17 km NE of San Gabriel Etla, 13 May 1985, López G. 258 (NY). Puebla (?): Orizaba, Engenio, Sierra de Cruz, Aug 1853, Muller s.n. (NY), Sinaloa; Cerro de la Sandia, NE of Panuco, 29-30 Aug 1935, Pennell 20050 (GH). Sonora: Puerta de Pinitos, 14 Oct 1890, Hartman 150 (GH); Bakachaka, Río Mayo, 5 Jul 1935, Gentry 1464 (GH,MO); ridge S of Arroyo Gochico, E of San Bernardo, 5-9 Aug 1935, Pennell 19531 (GH,NY). Veracruz: Mt. Orizaba, Mageyas to Lomogrande, 26 Apr 1938, Balls 4347 (GH).

UNITED STATES. Arizona: Santa Cruz Co., Santa Rita Mountains, 7000 ft, 25 Jul 1884, Pringle 8175 (NY) and 8174 (NY).

Eastwood (1909) recognized Castilleja nervata only from Chihuahua. The remainder of the species (as treated here) was identified by her as C. lithospermoides, although she noted that the two taxa were similar. The type of C.

lithospermoides, however, was collected in Hidalgo (north of the known range of C. nervata), and the type specimen (fiche) as well as the original illustration show clasping leaves and exserted corollas characteristic of C. scorzoneraefolia. Jiménez (1985) clearly used C. lithospermoides as the name for what is identified in the current study as C. scorzoneraefolia; the plants he identified as C. scorzoneraefolia, with acute calyx lobes and large anthers, are some other species.

The type of Castilleja cruenta (Chiricahua Mountains, Arizona), is typical of C. nervata; the plants from the Santa Rita Mountains, Arizona (Pringle 8174 and 8175), are atypical in their shallowly toothed floral bracts but otherwise so similar to C. nervata that they must be referred to it.

Castilleja nervata and C. scorzoneraefolia have closely contiguous geographic distributions (Map 1), and apparent intermediates may be found along the area where their ranges abut. The two species are sympatric in the area of Edo. México, Morelos, the north half of Oaxaca, and Puebla, the area of Volcán de Colima along the Jalisco-Colima border, the area of Mt. Tancitaro, Michoacán, and in southwestern Durango. Within C. scorzoneraefolia, scattered through its range, aspects of variability support an hypothesis of close relationship to C. nervata. Although the corollas are usually well exserted in C. scorzoneraefolia, they are sometimes nearly included, and although the vestiture is mostly of loose hairs, they may be distinctly hispid.

III. The identity of Castilleja bella

Castilleja bella has previously been known to occur on Cerro Potosí, Nuevo León (the type locality) and Cerro Peña Nevada (along the Nuevo León-Tamaulipas border) (McDonald 1990), and its presence is here recognized on the high peaks east of Saltillo, Coahuila (Sierra Coahuilón and Sierra La Marta). The extension of its known range to the latter area makes its distribution more typical of the majority of species of the alpine-subalpine flora of northeastern México (McDonald in press).

Castilleja bella Standley, Field Mus. Pub. Bot. 22:106. 1940. TYPE: MEX-ICO. Nuevo León: Mpio. Galeana, peak of Cerro Potosí, abundant in meadows above and below timber line, 21 Jul 1935, C.H. Mueller 2249 (HOLOTYPE: F; Isotype: MO!).

Caespitose perennials from a thick, straight taproot. Stems herbaceous, 2-6(-30) cm tall, stems and leaves very sparsely pilose with loose, vitreous hairs mostly 0.8-1.6 mm long, eglandular. Leaves 2-5 cm long, narrowly triangular, 3 veined, sessile, distinctly clasping, with 1-2 pairs of narrow lobes or the taller plants with at least the lower leaves entire. Floral bracts 23-28 mm

long, oblong lanceolate to obovate, 3 veined, 3-5 mm wide, with 1-2 pairs of narrow lobes, the upper 2/3 of each lobe red tipped. Calyx red and glandular at the apex, 28-36 mm long, equally divided, the primary lobes 6-10 mm long, the secondary lobes rounded and shallow, 1-2 mm long, sometimes completely absent. Corolla 28-38 mm long, the lower lip of 3, fleshy, green teeth 0.5-2.0 mm long, the galea 6-9 mm long, 25%-33% as long as the corolla, exserted from the calyx 1-6 mm. Chromosome number unknown.

High sierra of southeastern Coahuila (Sierra La Marta and Sierra Coahuilón), northcentral Nuevo León (Cerro Potosí), and southern Nuevo León and adjacent Tamaulipas (Cerro Peña Nevada) (Map 4), alpine and subalpine zones, 3000-3700 m; May-Jul(-Nov); at the crests of Sierra La Marta and Sierra Coahuilón among *Pinus culminicola* Andresen & Beaman and shrubs, pinefir meadows, pine-oak woods, 3016-3600 m; on Cerro Potosí in rocky, alpine meadows and edge of krumholz near the peak, into pine meadows below, 3350-3700 m; on Peña Nevada in the area of the highest peak, 3400-3600 m.

Additional collections examined: MEXICO, Coahuila: Mpio, Arteaga: Sierra Coahuilón, 17 Jun 1991, Hinton et al. 20998 (TEX); Sierra la Marta, 17 May 1981, Poole 2316 (TEX): Sierra la Marta, first peak E of Cerro Morro, 20 Jul 1985, McDonald 1685 (TEX). Nuevo León: Mpio. Dr. Arrovo, Sierra de Peña Nevada: north of Picacho de San Onofre, burned zone on W side, with dominant Ceanothus and Arctostaphylos, ca. 3400 m. 30 Nov 1984, McDonald & Gómez 1292 (TEX); Picacho de San Onofre, E side, ca. 3600 m, 5 Jul 1985, McDonald 1664 (TEX); Mpio. Galeana, Cerro Potosí: NE summit, 13 Sep 1960, Beaman 4456 (GH); near summit, 27 Aug 1987, Bogler & Atkins 162 (TEX); summit, 18 May 1982, Dorr 2277 (TEX); top, 28 Oct 1982, Grimes 2971 (TEX); Cerro Potosí ascent, 3350 m, 2 May 1969, Hinton et al. 17012 (TEX); [near summit], 21 Jun 1969. Hinton et al. 17109 (TEX); summit, 25 May 1969, Hinton 17049 (TEX); top, 23 Aug 1984, Lavin 4781 (TEX); alpine zone, 26 Oct 1984, McDonald & Gómez 1260 (TEX); alpine zone, 26 Jul 1985, McDonald 1788 (TEX); ascent of Sierra Potosi by the N hogback, abundant on the meadow at the peak and common in the forest immediately beneath, 26 Jul 1934, Mueller 1234 (GH, TEX); ascent of Sierra Potosí by the north hogback, common in all parts of the pine forest, 26 Jul 1934, Mueller & Mueller 1239 (GH, TEX); peak, 18 Jul 1938, Univ. Illinois Exped. 935 (GH, MO); summit, 20 Oct 1979, Warnock 2013 (TEX); summit, 24 Jul 1977, Wells & Nesom 235 (TEX). Tamaulipas: Mpio. Miquihuana, Cerro Peña Nevada, 1 Jun 1974. Patterson 1514 (TEX).

In the original description of *Castilleja bella*, Standley (1940, p. 106) quoted comments by the collector of the paratype regarding variation in the species: "A very conspicuous plant, abundant on the treeless peak, and extending down (equally abundant) into the pine forest and in grassy openings for over 300 meters. In exposed places only 2.5-5 cm high. In the shelter of the timber at times reaching a height of 12 cm, but even in such places most of the plants are low." The same variation in habit noted by Standley is confirmed by study of the numerous herbarium specimens by which this species is now represented. The plants are mostly acaulescent (2-6 cm tall) in alpine zones, but even on the peak (and near it) of Cerro Potosí, among acaulescent plants are individuals with stems commonly to 12 cm tall and ranging up to 30 cm (e.g., *Hinton* 17109, Mueller 1234, McDonald 1788, Bogler & Atkins 162). Plants with the typical, acaulescent habit occur on Cerro Potosí and Peña Nevada, but so far only taller plants have been collected from Coahuila.

Castilleja bella differs from C. scorzoneraefolia in its high elevation habitats, caespitose habit, with numerous branches arising immediately from a thick taproot, floral bracts (and sometimes upper leaves) with 1-2 pairs of narrowly lanceolate lobes, and sparsely villous, eglandular stems. The caespitose habit, however, as well as the reduced vestiture and similar taproots, are also found in some plants of C. scorzoneraefolia from Nuevo León and Coahuila, particularly at the upper range of elevation of that species. The primary distinction between C. scorzoneraefolia and the taller plants of C. bella is the lobing of the floral bracts and upper leaves. In Coahuila and Nuevo León, C. scorzoneraefolia occurs at 970-2700 meters elevation, with a few plants reaching as far up as 3400 meters. The lowermost elevation known for plants of C. bella is 3000 meters, but most occur above 3300 meters.

The similarities between Castilleja bella and high elevation C. scorzoneraefolia suggest that some gene flow may be occurring between the two taxa. In a few collections of relatively taller plants, some plants have lobed bracts, while others have entire bracts (e.g., Mueller & Mueller 1239-TEX lobed but Mueller & Mueller 1239-GH entire; McDonald 1695 and Hinton 17109, most plants with lobed bracts, few with entire). Somewhat arbitrarily, I have identified all plants from these populations as C. bella. On Peña Nevada, however, where C. scorzoneraefolia is common at lower elevations and extends upward to at least 3400 meters, the difference between it and C. bella is marked. No plants there of C. scorzoneraefolia produce lobed leaves or bracts and most of them are single or few stemmed from the base.

Castilleja bella is very similar to C. moranensis Kunth (=C. pringlei Fern. and C. schaffneri Hemsley), which is also primarily caespitose but shows the same variability in height as C. bella. Castilleja moranensis occurs in the states of Hidalgo, México, Morelos, Puebla, and Veracruz, where it is found in a variety of habitats in elevations ranging 2400-3700(-4000) meters. It is not clear whether C. bella and C. moranensis are sister species, with the caespitose habit and lobed floral bracts inherited from a common ancestor, or whether each species may have been independently derived from C. scorzoneraefolia. The two can be distinguished by the contrasts in the following couplet.

1. Calyx cinereous, the veins and lobe margins densely ciliate with stiffly

1. Calyx green, the veins and lobe margins sparsely pilose with loosely spreading, vitreous hairs; leaves mostly 4-6 mm wide at midleaf. C. bella

IV. The identity of Castilleja aspera

- Castilleja aspera Eastwood, Proc. Amer. Acad. Arts 44:580. 1909. TYPE: MEXICO. Chihuahua: Sierra Madre near Colonia García, 2287 m, 3 Jun 1899, C.H.T. Townsend & C.M. Barber 449 (HOLOTYPE: GH!).
 - Castilleja nelsonii Eastwood, Proc. Amer. Acad. Arts 44:579. 1909. LECTOTYPE (designated here): MEXICO. Chihuahua: Mount Mohinora, 1 Sep 1898. E. W. Nelson 4895 (GH!; Isolectotypes: GH!, US,US-photo at GH!). The lectotype and isolectotype sheets at GH apparently hold the upper portion and base of a single plant, respectively, perhaps mounted separately by mistake.

Plants perennial. Stems erect, 18-40 cm tall, sometimes few branched from the base, invested with an understory of minute, eglandular, spreading hairs, the overstory absent or nearly so to much longer, stiffly spreading, vitreous hairs, the latter often gland tipped. Leaves sparsely and minutely scabridulous to sparsely glandular pilose, oblanceolate or narrowly oblong lanceolate to elliptic, 18-62 mm long, 5-13 mm wide, clasping to subclasping, sometimes barely so, 3(-5) veined, the veins strongly raised on the abaxial surface, margins of lower leaves sometimes with short, spreading cilia. Floral bracts entire, 3 veined, 5-8 mm wide, the uppermost red tipped. Calyces red and glandular at the apex, 18-25 mm long, tubular or narrowing toward the apex, the primary lobes 5-9 mm long, with acute apices, nearly equal in length, the secondary lobes 2-4 mm long, triangular. Corollas 20-32 mm long, the lower lip of 3, thick, green teeth ca. 2 mm long, the galea 8-12 mm long, pilose and glandular dorsally, ca. 33%-40% as long as the corolla, exserted 2-10 mm from the calyces. Chromosome number unknown.

Northern Chihuahua to central Durango (Map 2); pine-oak to pine woodlands, 2100-2670 m; Jul-Sep.

Additional collections examined: MEXICO. Chihuahua: Mpio. Bocoyna, W of Creel on mesa and E slope above Río Oteros, 1 Aug 1977, Bye & Weber 7823 (GH); near Colonia García, 25 Aug 1899, Nelson 6101 (GH); S of Colonia García, 23 Sep 1934, Pennell 19131 (GH); Mpio. Guerrero, 7 mi E of Tomochic on road to La Junta and Cuauhtemoc, 5 Oct 1986, Spellenberg et al. 8880 (TEX); near Colonia García. 4 Jun 1899, Townsend & Barber 8 (GH,MO); near Colonia García, 9 Aug 1899, Townsend & Barber 250 (GH,MO). Durango: Mpio. Santiago Papasquiaro, ca. 22 air km WNW of Santiago Papasquiaro, 25 Aug 1983, Worthington 11437 (NY).

The vestiture of Castilleja aspera appears to be somewhat more variable than normal for most species of the genus. The type of C. nelsonii represents an extreme condition with strongly reduced vestiture, the leaves only sparsely and minutely scabrid. Worthington 11437 from northern Durango is similar to the type of C. aspera and other plants from around Colonia García, Chihuahua, except for Pennell 19131 and Bye & Weber 7823, which are more like the type of C. nelsonii. Additionally, the secondary calyx lobes of C. nelsonii (the type) are well differentiated but not sharply acute as in the other specimens of C. aspera, and it was apparently solely on this basis that Eastwood separated C. nelsonii from C. aspera. Nevertheless, considering their morphological similarity in all other features, as well as their geographical identity, the two are treated here as conspecific.

Plants from southcentral Durango have been identified by Eastwood (1909) and others as *Castilleja aspera*, but in the present study, they primarily are placed with following species, which is previously undescribed.

Castilleja durangensis Nesom, sp. nov. TYPE: MEXICO. Durango: ca. 5 km NE of El Salto, Rte 40 near K 1059, pine woods and wet llanos, under pine trees, with Eryngium, Commelina, Ranunculus, Calochortus, and Lobelia, 2780 m, 6 Aug 1966, R.W. Cruden 1160, voucher for chromosome count of n=12 [Heckard 1968, as Castilleja aspera] (HOLO-TYPE: TEX!; Isotype: GH!)

Castillejae asperae Eastwood similis sed vestimento eglanduloso dense brevihispidulo et foliis angustioribus absque venis valde elevatis differt.

Perennials, apparently from shallow, slender, woody rhizomes; stems, leaves, and bracts evenly and densely hispidulous with sharp pointed, spreading, sometimes slightly deflexed hairs 0.1-0.3(-0.5) mm long, eglandular. Stems erect, unbranched, 13-40 cm tall. Leaves ascending, often distinctly recurved, linear to oblong lanceolate, basally rounded and subclasping, 2-5 cm long, 2-5 mm wide, 3-(-5) veined. Mature inflorescence/infructescence (3-)6-15 cm long; floral bracts entire, narrowly oblanceolate to narrowly obovate. 3 veined, 5-8 mm wide, red tipped. Calyces red and glandular at the apex. 18-22 mm long, tubular, the primary lobes 6-7 mm long, with acute apices, nearly equal in length, the secondary lobes 1-4 mm long, triangular. Corollas 21-25 mm long, the lower lip of 3, thick, green teeth 1-2 mm long, the galea 7-10 mm long, pilose and glandular dorsally, ca. 33%-40% as long as the corolla, exserted 2-6 mm from the calyces. Chromosome number, n=12 (voucher is type collection). Southcentral Durango (Map 2); grassy slopes, sometimes wet, in pine and pine-oak woodlands; (2300-)2500-2850 m; Jun-Sep(-Oct).

Additional collections examined: MEXICO. Durango: 32.7 mi W of Durango, well spaced pine-oak forest on gentle slopes of loamy soils over volcanic rock, 23 Jul 1955, Johnston 2686 (TEX); 39 mi E of El Salto, 7 Jun 1967, Moldenke 1573 (NY, mixed with Castilleja scorzoneraefolia); 4 mi E of El Salto on road to Durango, 22 Aug 1957, Ornduff & Solbrig 4639 (GH); Otinapa, 25 Jul-5 Aug 1906, Palmer 367 (GH,MO, cited by Eastwood as C. aspera); El Salto (Aserraderos), grassy pineland, 28 Aug 1934, Pennell 18294 (GH-with 1 plant of C. nervata); Metates, N of Cueva, pineland on mt. slope, 29-30 Aug 1934, Pennell 18393 (GH-with 1 plant of C. nervata); El Salto (Aserraderos), grassy pineland, 31 Aug 1934, Pennell 18499 (GH); El Salto (Aserraderos), mossy, grassy pineland, 1 Sep 1934, Pennell 18542 (GH); El Salto (Aserraderos), mossy, marshy glade in pineland, 1 Sep 1934, Pennell 18549 (GH); 3 mi E of El Salto off Hwy 40, 21 Sep 1974, Rollins & Roby 7426 (GH-with 1 plant of C. saltensis Eastwood, NY); 28 mi E of El Salto, 23 Jul 1976, Walker 76H23 (MO).

The plants of Castilleja durangensis are confined to a small area of southcentral Durango (Map 2). They are somewhat similar in habit to C. scorzoneraefolia, but their evenly and densely short hispidulous vestiture, lacking glandular hairs, separates them from all other Mexican species. The secondary calyx lobes of C. durangensis are triangular with acute apices, a distinctive feature shared with plants of C. aspera and perhaps indicating a close relationship between the two. Plants of C. aspera are generally taller and the leaves broader than in C. durangensis and typically produce a vestiture more similar to that of C. scorzoneraefolia. The vestiture of the two branches of Moldenke 1573 (C. durangensis) is slightly glandular, probably reflecting the genetic influence of nearby C. scorzoneraefolia, plants of which are mounted on the same sheet.

V. A new species related to Castilleja lanata

Castilleja galehintoniae Nesom, sp. nov. TYPE: MEXICO. Nuevo León. Mpio. Galeana, San José de Las Joyas, 2480 m, common on bare hillside, flowers yellow, 5 Jul 1983, *Hinton et al. 18422* (HOLOTYPE: TEX!; Isotypes: ANSM!,MEXU!,NY!,UC!).

Differt a *Castilleja lanata* A. Gray statura breviore, bracteis ac calycibus absque apicibus rubris, et corollis brevioribus labio infero loborum longorum linearium composito.

Perennials, arising from slender, woody, rhizomelike caudex branches, the stems 5-25 cm tall; stems, leaves, bracts, and calyces evenly and densely tomentose-villous with whitish, long, minutely filiform and intertwined hairs, at least many of these originating as lateral branches of dendritic hairs, mostly with one node and several branches, minute glands sometimes apparent but never prominent beneath the other hairs. Leaves densely arranged on the stems, linear, 3 veined, 1.5-4.5 cm long, 1.0-1.5(-2.5) mm wide. Mature inflorescence/infructescence 2-4 cm long; floral bracts 13-22 mm long, abruptly differentiated from the leaves, linear with a pair of linear, lateral lobes originating at about midlength. Calyces 15-18 mm long, tubular or slightly narrowing toward the apex, equally divided, the primary lobes 6-7 mm long, the secondary lobes rounded, barely developed, 0.5-1.0 mm long. Corollas 15-20 mm long, yellow with blackish veins, the lower lip of 3, thick, linear lobes 2-4 mm long, the galea 10-11 mm long, 50%-55% as long as the corolla, dorsally glandular but without other hairs, exserted 1-4 mm from the calyx. Chromosome number unknown.

Nuevo León endemic (Map 3); apparently restricted to gypseous substrates, in matorral, grasslands, cedar savannas, open oak woods; 1300-2480 m; Apr-Aug(-Oct).

Additional collections examined. MEXICO. Nuevo León: Mpio. Aramberri, E of Aramberri, 14 May 1991, *Hinton et al. 20933* (TEX). Mpio. Galeana: above E Carrizo, 16 Oct 1983, *Hinton et al. 18149* (TEX); S slope of Potosí, 25 Jun 1983, *Hinton et al. 18449* (TEX, dup); San José Las Joyas, 23 Jul 1983, *Hinton et al. 18530* (TEX, dup); road to Dieciocho de Marzo, 11.5 mi E of jct with Hwy 57 at San Rafael, 28 mi NW of Dieciocho de Marzo, 4 Jul 1985, *Luckow 2651* (TEX); 15 mi SW of Galeana, above Encinal, 19 May 1934, *Mueller 485* (GH,TEX); ca. 15 mi SW of Galeana, Taray to Alamar at la Mesa de la Zorra, 20 Jul 1934, *Mueller 1109* (GH,TEX); Arroyo Hondo, Hacienda San José de Raices, 31 Jul 1935, *Mueller 2307* (GH,MO,TEX); Hacienda Pablillo, 1 Aug 1936, *Taylor 41* (MO,TEX); Hacienda Pablillo, 26 Aug 1936, *Taylor 221* (TEX).

The new species is endemic to southcentral Nuevo León, México (Map 3), and it is named for Gale Hinton, daughter of Jaime Hinton and brother of George, who loved the mountains and flowers around her home in the same area of Nuevo León. *Castilleja galehintoniae* is clearly most closely related to *C. lanata*, which also produces a dense vestiture of branched hairs, mostly linear leaves, an evenly divided calyx, and corollas with a lower lip of 3 linear lobes. The two species differ in features noted in the following couplet.

- 1. Stems 5-25 cm tall; floral bracts with lobes usually originating from near the middle, apices densely lanate, the vestiture similar from base to tip;



Map 3. Distribution of Castilleja galehintoniae and C. lanata in Nuevo León and closely adjacent areas. Arrow shows the location of the type collection of C. galehintoniae; the type of C. lanata is from Texas.



Map 4. Distribution of *Castilleja bella*. Arrow shows the location of the type collection.

While Castilleja lanata is somewhat variable in size, it is consistently and easily recognizable as a single species over its entire geographic range. It occurs widely in the southwestern United States (Arizona, Colorado, New Mexico, and southwest Texas) and northern México (from Sonora, Chihuahua, and northern Durango to Coahuila, northern Zacatecas, San Luis Potosí, and southern Tamaulipas). It is also relatively common in western Nuevo León, where its geographic range touches that of C. galehintoniae, and the two are apparently even slightly sympatric in that area (Map 3). Several collections from the area of sympatry can be identified as possible intermediates (e.g., Cowan 4626-TEX, near the village of El Potosí, and some plants of Hinton 18449-identified here as C. galehintoniae), but where the two taxa meet, the transition in morphology for the most part appears to be abrupt, with C. galehintoniae strikingly different in appearance from C. lanata. Putative intermediates have shorter calvees and corollas than normal for C. lanata, but the floral bracts and calvces are distally distinctly red with somewhat reduced vestiture. Some other collections of C. lanata from this area also are unusual in producing lobed upper leaves, although the origin of this variability is not clear.

- VI. A new species of uncertain relationships
 - Castilleja dendridion Nesom, sp. nov. TYPE: MEXICO. Oaxaca: Dist. Centro, 10 mi NE of Oaxaca along Hwy 175, pine-oak forest on steep slopes, 2 Sep 1982, L.E. Gieschen s.n. (HOLOTYPE: TEX!).

A speciebus ceteris *Castillejae* dignoscenda vestimento denso trichomatum dendriticorum flavipigmentosorum, foliis confertim dispositis linearibus integrisque, bracteis floralibus lobis ad apicem expansis dentatisque, et lobis calycum pariter divisis.

Shrubby perennials, the stems basally woody and at least 40 cm tall; stems, leaves, floral bracts, and calyces densely invested with multicellular, dendritic hairs 0.2-1.0 mm high, branching 2-4 times above the 1-2 basal (stipe) cells, each hair with 2(-3) branches at each cellular node, the hairs of the stems and leaves usually prominently yellow pigmented, giving the whole plant a yellowish cast. Leaves linear-filiform, 9-17 mm long, ca. 1 mm wide, not at all basally widened or clasping, densely arranged (3-6 per cm of the stem) with axillary tufts of smaller leaves at nearly every node. Mature inflorescence/infructescence 4-10 cm long. Floral bracts abruptly differentiated from

the leaves, 14-15 mm long, 2-3 mm wide at the base, with a pair of linearlanceolate lobes arising 2-3 mm from the base, all 3 lobes red and abruptly broadened apically, the apices truncate and shallowly toothed. Calyces red tipped and glandular, 13-15 mm long, tubular, equally divided, the primary lobes 6-8 mm long, secondary lobes deltate, ca. 1 mm long. Corollas 14-15 mm long, lower lip of 3, thick teeth ca. 2 mm long, the galea 8-9 mm long, ca. 60% as long as the corolla, dorsally glandular but without other hairs, exserted (0-)1-2 mm from the calyx. Chromosome number unknown.

Known only from the type collection (Map 1), which comprises a single, though full and densely floriferous, branch.

Castilleja dendridion is so distinctive in its morphology that no other species in the genus can be easily identified as closely related. Other species of Castilleja produce dendritic hairs (see Nesom 1991, as well as C. galehintoniae, above), but such highly elaborated hairs are not found elsewhere in the genus. Further, the peculiar morphology of the floral bracts apparently is found only in this species. The evenly divided calyx at least suggests that C. dendridion belongs among the species placed by Eastwood (1909) in sect. Euchroma (Nutt.) Benth., although the overview of the subtribe Castillejinae by Chuang & Heckard (1991) suggests that this morphology is probably primitive within the subtribe. Chuang & Heckard (1991) noted that overemphasis of the nature of calyx incision in classification probably results in the recognition of artificial groups, and they observed that satisfactory arrangement of Castilleja species into groups awaits a more detailed knowledge of the genus. All taxa treated in the present study are in Castilleja subg. Castilleja sensu Chuang & Heckard.

ACKNOWLEDGMENTS

I thank Dr. T.I. Chuang and Dr. B.L. Turner for their comments on the manuscript and the staffs of GH,NY, and PH for loans of specimens. Specimens from MO were studied on a recent visit there.

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